# Shell Growth and Repair in the Gastropod *Tegula funebralis*

(Mollusca: Gastropoda)

BY

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(3 Text figures; 2 Tables)

Shells of *Tegula funebralis* (A. Adams, 1854) inhabiting the intertidal areas of Mussel Point, Pacific Grove, California, are rarely found to have more than four whorls, irrespective of the size of the snail, due to heavy erosion of the upper parts. Questioning the nature of repair of erosion damage led to a consideration of the more general question of shell repair in *T. funebralis*. Fretter & Graham (1962) discuss shell formation in prosobranch molluscs, but little is understood of shell repair mechanisms.

*Tegula funebralis* lives in what is essentially a tapered tube, closed at the small end. This is clearly seen in Figs. 1 and 2. Macroscopically, there are three layers in the shell. The thin, transparent periostracum on Mussel Point specimens is present only on the body whorl near the shell aperture, if at all. Underlying the periostracum is a black prismatic layer. These two layers are secreted only by the mantle margin. Innermost is a thick nacreous layer, white over most areas, but sometimes yellow or greenish in the upper whorls. Slides of decalcified shells embedded in paraffin show the laminar character of the nacreous matrix.

Most of the specimens of *Tegula funebralis* from Mussel Point have shells which are conspicuously eroded. Although some of the erosion appears to be due to the radular action of predaceous snails, boring of bryozoans and polychaetes, or mechanical wear, all save a minority of *T. funebralis* (individuals measuring 5 mm or less at the greatest basal diameter) are pitted over most of the eroded surface. Under 30x magnification, this damage closely resembles that caused by a fungus described as infesting shells of marine animals by Bonar (1936). Attempts were made to culture the fungus on *T. funebralis* on a medium of 100 ml sea water, 1 gm $CaCO_3$, 1 ml 1 M $NaNO_3$, 1 ml 1 M $KH_2PO_4$, 1.5 gm agar, 1 gm humus, 5 gm *T. funebralis* shell, finely ground, 0.1% glucose, and 0.01% yeast extract. The fungus in culture shows chlamydospores (see Fig. 3) which differ from those on the species raised by Bonar, and also from those found by Johnson (1962) in a fungus growing on smooth jingle shells (*Anomia simplex* d'Orbigny) from Pivers Island beach, North Carolina.

Normal shell growth in *Tegula funebralis* was measured for a fifteen-day period (May 14-29, 1963) on individuals ranging 13.0-27.5 mm in greatest basal diameter. Measurements were made with an ocular micrometer of growth increments on the outer lip of the aperture, secreted on

Explanation of abbreviations used in the figures:
a - shell aperture; an - anus; cm - columellar muscle; ct - ctenidium; e - eye; f - foot; g - gonad; h - heart; ht - head tentacle; k - kidney; mc - mantle cavity; op - operculum; os - osphradium; r - rectum; s - shell; sc - spiral caecum; st - stomach.

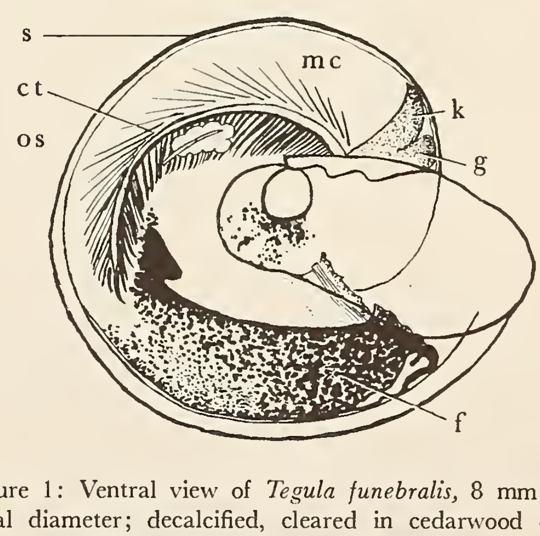


Figure 1: Ventral view of *Tegula funebralis*, 8 mm in basal diameter; decalcified, cleared in cedarwood oil, and with black prismatic layer removed.

Table 1

Growth Studies on the Shell of *Tegula funebralis*

| Snail no. | Greatest basal diam. (mm) | *Addition to Shell at Aperture on Successive Days* (mm) | | | | | | | | | Average growth per day |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | 1 | 2 | 5 | 6 | 8 | 9 | 11 | 12 | 15 | |
| 1 | 13.0 | 0 | 0 | 0 | — | — | 0 | — | .060 | .090 | .006 |
| 2 | 13.5 | 0 | 0 | 0 | — | — | .090 | — | .120 | .210 | .014 |
| 3 | 16.0 | 0 | 0 | 0 | — | — | .030 | — | .060 | 0 | .004 |
| 4 | 17.0 | 0 | 0 | 0 | — | — | .030 | — | .060 | .090 | .006 |
| 5 | 17.0 | 0 | 0 | 0 | — | — | .030 | — | .060 | 0 | .004 |
| 6 | 18.0 | 0 | 0 | 0 | 0 | — | 0 | — | 0 | .030 | .002 |
| 7 | 18.0 | 0 | 0 | 0 | — | — | 0 | — | .030 | .060 | .004 |
| 8 | 19.0 | 0 | 0 | 0 | — | — | — | — | 0 | X | 0 |
| 9 | 20.0 | 0 | 0 | 0 | — | — | .090 | — | .120 | 0 | .008 |
| 10 | 20.5 | 0 | 0 | 0 | — | — | .090 | — | .120 | 0 | .008 |
| 11 | 21.0 | 0 | 0 | 0 | — | — | X | | | | 0 |
| 12 | 21.0 | 0 | 0 | .100 | — | 0 | — | .165 | — | 0 | .011 |
| 13 | 22.0 | — | .033 | .100 | — | .132 | — | .165 | — | 0 | .011 |
| 14 | 23.0 | 0 | 0 | 0 | — | — | .060 | — | .090 | 0 | .006 |
| 15 | 23.0 | 0 | 0 | 0 | — | — | .090 | — | .120 | .150 | .010 |
| 16 | 23.0 | 0 | 0 | 0 | — | — | .030 | — | .060 | .090 | .006 |
| 17 | 23.0 | 0 | 0 | 0 | — | -- | .030 | — | .060 | 0 | .004 |
| 18 | 23.0 | 0 | 0 | — | — | — | — | 0 | — | 0 | 0 |
| 19 | 24.0 | 0 | 0 | 0 | — | — | .030 | — | .060 | .090 | .006 |
| 20 | 24.0 | 0 | 0 | 0 | — | — | 0 | — | 0 | — | 0 |
| 21 | 24.0 | 0 | 0 | 0 | 0 | — | .060 | — | .090 | 0 | .006 |
| 22 | 24.5 | 0 | 0 | 0 | — | — | .060 | — | .090 | .120 | .008 |
| 23 | 25.0 | 0 | 0 | 0 | — | — | .015 | — | .030 | .120 | .008 |
| 24 | 25.0 | 0 | 0 | 0 | — | — | .030 | — | .090 | .120 | .008 |
| 25 | 25.5 | 0 | 0 | 0 | 0 | — | 0 | — | .030 | 0 | .002 |
| 26 | 25.5 | 0 | 0 | .132 | — | — | — | .165 | — | 0 | .011 |
| 27 | 27.5 | 0 | 0 | 0 | 0 | — | .060 | — | X | | .007 |
| 28 | 27.5 | 0 | 0 | 0 | — | — | .060 | — | .120 | 0 | .008 |

Legend:
- O no change since last observation
- — no observation
- X dead

top of a baseline of fingernail polish painted on the edge of the aperture at the beginning of the study. Results are shown in Table 1. The average overall addition to shell aperture was six microns per day, but growth occurred in spurts, not evenly each day. Total growth over the fifteen-day period did not measurably affect the greatest basal diameter of the shells.

In order to assess the ability of *Tegula funebralis* to repair damage incurred to the shell, snails were operated on in various ways, inflicting different types of shell damage, as indicated in Table 2. Five individuals were operated in each way. The holes (windows) made in the shell back of the aperture were ground on an emery wheel, care being taken to keep the shell wet and cool, and the internal tissues intact. Table 2 gives the average change in each group on successive days. The range of variation within each group was not so great as to make the average irrelevant. In every case of damage to the shell

## Table 2

Repair of Shell Damage in *Tegula funebralis*

| | Type of Operation | Repair on Successive Days After Operation (mm Added to Shell at Aperture) | | | | | |
|---|---|---|---|---|---|---|---|
| | | 2 | 5 | 6 | 8 | 11 | 15 |
|  | control (no operation; normal growth at aperture lip recorded) | O | .1 | - | O | .165 | O |
|  | mantle margin slit | O | .2mm notch | notch filled | | | |
|  | 2.6 mm notch filed in edge of shell aperture | .066mm of notch filled | .240mm of notch filled | - | .388mm of notch filled | .479mm of notch filled | .677mm of notch filled |
|  | window over visceral hump | M | $CaCO_3$ | O | O | 2 $CaCO_3$ layers | O |
|  | window over heart and kidney area | M | $CaCO_3$ | - | X | | |
|  | window over mantle cavity | O | .18 added to hole edge | - | .198 | .353 | .397 |
|  | shell cracked (with a vise) | M | $CaCO_3$ | - | white nacreous secretion over crack (xx) | O | O |
|  | shell broken at aperture (with pliers) | T | .187 | O | .221 | .386 | .354 |
|  | shell aperture ground off | T | .333 | - | .353 | .397 | .583 |

O no change since last observation
\- no observation
T just visible trace of nacreous layers secreted
M soft, membranous layer secreted over opening
$CaCO_3$ dead
X calcium carbonate embedded in soft layer

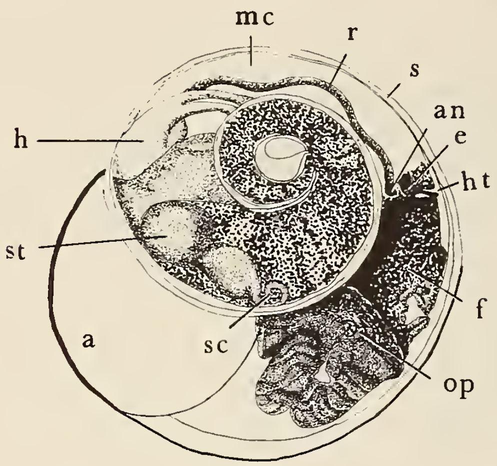


Figure 2: Dorsal view of *Tegula funebralis,* same individual as shown in Figure 1.

aperture, growth of the damaged part proceeded faster than the growth at apertures of undamaged controls. All such operations on the apertures were repaired by the folds at the border of the mantle. The same was the case with the windows over mantle cavities. New shell material included a black prismatic layer.

When the mantle margin was slit in an otherwise undamaged specimen, within two days a notch appeared in the shell aperture at the point apposed to the incision. It is not clear whether the notch was due only to lack of growth, or in part due to active resorption of shell at the point. but within six days the notch was repaired.

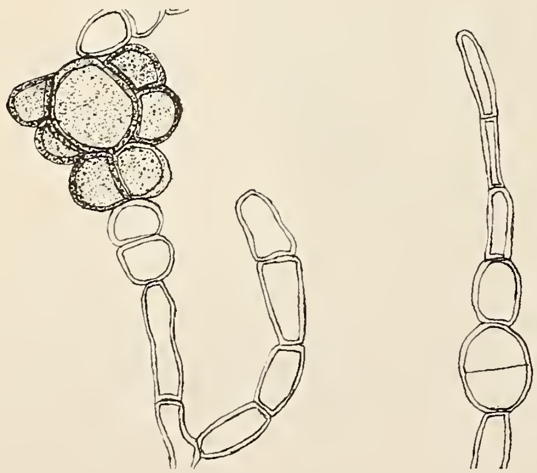

Figure 3: Fungus found on *Tegula funebralis* shell; part of mycelium with chlamydospores.

Snails with openings over the visceral hump first secreted a soft, membranous layer across the inside of the hole; this later became impregnated with calcium carbonate. Successive layers, similar in appearance, were built up beneath the first layer, which bulged through the opening. After thirty days (April 30-May 29, 1963), one specimen had plugged the shell window with a hard patch of white material, apparently calcium carbonate embedded in an organic matrix. The patch protruded through the opening like a bubble, and was translucent at the periphery, opaque in the center portion. Of three females and two males, with windows cut over the visceral hump, the females began repair sooner than the males. None of the snails with windows over the visceral hump died, although the gonad was frequently ruptured. On the other hand, animals with the shell damaged by grinding a hole over the region of the heart and kidney died in all cases except one. Death was due not to the operation, but to the later rupture of the kidney or pericardial sac against the sharp edge of the opening produced by the operation. One specimen which lived an entire month with this operation failed to successfully repair the damage, for each time the soft membranous layer covering the hole became embedded with calcium carbonate, it was sloughed off through the opening.

In the "windowed" animals, even where the holes penetrated yellow and green layers, I observed no secretion of yellow or green material by the mantle covering the body, nor is it secreted by the mantle margin. Secretions by other than the mantle margin were always either transparent membranous layers or white inorganic material. However, natural repair does show yellow or green material, particularly in eroded areas at the shell apex. Perhaps the inner layers of nacreous material are dyed by pigments secreted by the visceral hump, specifically either the digestive gland or the gonad (see McGee, 1964).

Cracked shells were bound firmly together in a solid unit within five days by a calcium carbonate-embedded membrane on the inner surface. Additional white nacreous material was laid over the outer surface of the crack within eight days where the break passed through the underside of the body whorl adjacent to the shell aperture.

## SUMMARY


1. Shell erosion is caused by the activities of several animals (bryozoans and polychaetes), by mechanical wear, and by a fungus, which was cultured on agar plates.
2. Normal shell growth, recorded over a period of fifteen days in twenty-eight animals, was intermittent, but averaged six microns per day added to the outer lip of the aperture.

3. Repairs to shells damaged mechanically, by filing the aperture, grinding holes in the body and upper whorls, and by cracking in a vise are described.


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# The Dispersal of Young of the Commensal Gastropod *Crepidula adunca* from its Host, *Tegula funebralis*


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(4 Text figures)

## INTRODUCTION

*Crepidula adunca* SOWERBY, 1825 is a protandric marine prosobranch commonly found on the shells of *Tegula funebralis* (A. ADAMS, 1854), both when the latter is occupied by the snail and when it is occupied by *Pagurus* spp. MORITZ (1938) gives the range of *C. adunca* as being similar to that of *T. funebralis*: from Vancouver, British Columbia, to the tip of Lower California. CONKLIN (1897) has followed the cell lineage of *C. fornicata* and *C. plana*, and MORITZ (1938, 1939) has treated the anatomy and organogenesis of *C. adunca*.

*Crepidula adunca* undergoes a very direct development from large, yolky eggs which are brooded by the female. The hatching young crawl out of the egg cases as juveniles which are similar to adults. At hatching there may be from 150 to 200 young released. Although no pelagic stage is present, the adult population of *C. adunca* is quite well dispersed over the *Tegula funebralis* population near the Hopkins Marine Station, Pacific Grove, California. The number of adult *C. adunca* per *T. funebralis* shell is relatively low (eight was the maximum number seen) as compared to the large number of young per brood. Clearly, the young become dispersed to new hosts without benefit of a pelagic stage. How this is accomplished is the subject of the present investigation.

## HATCHING

*Crepidula adunca* breeds the year round (MORITZ, 1938). The animals used were gathered from Mussel Point, Pacific Grove, California. *Tegula funebralis* with the brooding *Crepidula* females were kept in glass finger bowls at 12 to 18° C. Young when hatched were kept similarly. All young used in all experiments were hatched without human assistance, both to avoid harming the young through attempts to liberate them artificially, and to establish their age, as the period of development to hatching is not known.

In the four cases where hatching was observed, young *Crepidula adunca* were released between 8:30 and 10:30 a. m. The egg cases are attached by individual stalks to one spot on the *Tegula funebralis* shell. immediately ventral and posterior to the head and anterior to the foot of the female *C. adunca*. Normally, the female's shell is lifted no more than 0.5 mm above the substrate, only enough to allow water to flow through the mantle cavity for filter-feeding and respiration. During hatching, however, the female intermittently lifts her shell 1 to 3 mm above the substrate, for periods which varied from 3.5 seconds to about 4 minutes. Then with a forward and downward motion of her head over the egg cases, the female pushes out those of her young which are loose